

THE EVOLUTION OF SEED MORPHOLOGY IN DOMESTICATED *Chenopodium*: AN ARCHAEOLOGICAL CASE STUDY

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ABSTRACT.—A large body of data on several key morphological characters has been compiled through examination of collections of archaeological *Chenopodium* from eastern North America. Contrary to expectations based on change in certain other seed crops, the patterns of variation observed in *Chenopodium* do not reflect a gradual evolution of seed morphology away from the wild type. Evidence for decreasing levels of morphological variability in the evolving domesticate is likewise minimal. These findings demonstrate that the rate and character of crop evolution as revealed in the archaeological record can be expected to vary considerably among taxa.

RESUMEN.—Se ha compilado un extenso ouerpo de datos sobre varios caracteres morfológicos clave mediante el examen de colecciones de *Chenopodium* arqueológico del este de Norteamérica. Contrariamente a las expectativas basadas en el cambio en ciertos otros cultivos de semilla, los patrones de variación observados en *Chenopodium* no reflejan una evolución gradual de la morfología de las semillas en creciente distancia del tipo silvestre. La evidencia de niveles decrecientes de variabilidad morfológica en la especie domesticada en evolución es asimismo mínima. Estos resultados demuestran que puede esperarse que la tasa y el carácter de la evolución de los cultivos, tal y como se revela en el registro arqueológico, varíen considerablemente entre taxa distintos.

RÉSUMÉ.—Un large ensemble de données concernant plusieurs caractères morphologiques importants a été recueilli en examinant des collections de *Chenopodium* de l'est de l'Amérique. Contrairement aux attentes basées sur les changements dans certaines espèces de graines cultivées, l'évolution de la morphologie des graines de *Chenopodium* à partir du type sauvage ne semble pas progressive, d'après les modèles de variation observés. Il est aussi évident que le niveau de variabilité morphologique évident dans l'évolution des types domestiqués diminue peu. Ces résultats démontrent que le rythme de modification et le caractère de l'évolution des types domestiqués, vus à travers les données archéologiques, doivent varier considérablement entre taxa.

INTRODUCTION

The origins and development of plant husbandry and its social, economic, and ecological consequences for past cultural systems have long been of interest to anthropologists. Consequently, much effort has been devoted to identifying the archaeological correlates of the initiation of food production. Often the best evi-

dence of this sort is found in the form of distinctive morphologies of cultigens that develop in the context of domestication, frequently as a result of the loss, reduction, or augmentation of particular anatomical structures. As a result of the utility of such traits as temporal markers for the origins of agriculture, analyses of cultigen morphology frequently emphasize their presence or absence rather than the details of their variation in space and time. However, more precise analyses of cultigen morphology do hold considerable potential as an empirical basis for inferences about various aspects of past human behavior. For example, compilations of morphometric data from the eastern United States have been used to trace the intensification of relationships between humans and weedy annuals (Fritz and Smith 1988; Smith 1987, 1989; Yarnell 1972, 1978).

Two aspects of crop evolution are especially amenable to examination using archaeological data. These are the rate and magnitude of change in characters linked to domestication (such as fruit size and seed coat thickness) and the variability exhibited by those same characters. In particular, researchers have been motivated to ask whether continuously varying traits such as fruit size changed gradually over time in a more or less linear direction, or rapidly, establishing a clear dichotomy between early and late forms. Also of interest is whether there was a tendency for domesticated populations to be less morphologically variable than their wild relatives, and if so how this might be explained as a result of selection in human-modified environments. The answers to these questions regarding the path taken by crop evolution have important implications both for the evolutionary history and ecology of particular plant species and the study of their relationships with human groups.

A large body of archaeological data from eastern North America pertinent to these research questions has accumulated in recent years. Archaeological evidence indicates that at least three weedy native annuals (sunflower, *Helianthus annuus* L.; sumpweed, *Iva annua* L.; and chenopod or goosefoot, *Chenopodium berlandieri* Moq.) were brought under domestication in the region before 1500 B.C. (Crites 1993; Smith 1987, 1989), although for chenopod the possibility of a Mesoamerican derivation remains to be fully evaluated on phylogenetic grounds (Wilson 1981, 1990). In the case of sunflower and sumpweed, evidence for domestication takes the form of a gradual increase in achene size that has been observed in archaeological material (Asch and Asch 1985b; Smith 1987; Yarnell 1972, 1978). In contrast, domesticated taxa within *Chenopodium* are primarily distinguished from their wild relatives by possession not of unusually large seeds, but of a complex of traits linked to the reduction of the seed coat. Both dark-seeded and pale varieties, which differ morphologically in the degree of seed coat reduction and the resulting color of the fruits, have been documented prehistorically in eastern North America (Fritz and Smith 1988). Although the pale phenotype is not known in wild populations (Wilson 1981), the dark-seeded cultigen is nearly indistinguishable from a form that occurs, albeit usually at low frequencies, in the wild.

This study applies morphometric data on eastern North American *Chenopodium* to the examination of the rate and character of the evolution of its cultigen forms. The problem is first addressed through documentation of changes in the thickness of the seed coat and other characters thought to be closely linked to selection in the context of domestication. Next, evidence for reduction in mor-

phological variability within domesticated chenopod populations is reviewed. Finally, the implications of temporal patterns of morphological variation in this species for human behavior are discussed.

PREVIOUS RESEARCH

Establishment of the domesticate status of Chenopodium.—*Chenopodium* seeds were found by Gilmore (1931) and Jones (1936) to be both ubiquitous and abundant among organic materials from dry rockshelters in eastern Kentucky and the Ozark uplands. However, it was not until the advent of flotation recovery of archaeological plant remains in the Eastern Woodlands that *Chenopodium* was found to be common at open sites as well. As evidence accumulated indicating that this plant (along with a number of other grain-producing species) was utilized well before the appearance of maize in the archaeological record, interest was quickly renewed in the hypothesized indigenous "Eastern Agricultural Complex." It was in the context of this debate that Asch and Asch (1977) set out to examine evidence of distinctive morphology in archaeological *Chenopodium* from the region. They concluded that the rockshelter specimens studied by Gilmore and Jones fell within the range of variability for modern nondomesticated populations, despite their tendency to display atypical frequencies of certain traits (e.g., truncate fruit margins and reddish coloration). Even the criterion of seed size, so useful for determining domesticate status in many taxa, failed to distinguish the archaeological specimens from wild ones when previously misidentified seeds of poke (*Phytolacca americana*) were eliminated from consideration.

In the 1980s the cultigen status of *Chenopodium* in the Eastern Woodlands was reassessed. The result of this reevaluation, pioneered by Hugh Wilson (1981) and Bruce Smith (1984, 1985a, 1985b) was that *Chenopodium* had indeed undergone morphological change prehistorically. However, instead of increased seed size, reduction of the seed coat and associated modifications of fruit margin configuration and cross-sectional shape were found to distinguish both extant cultivars of *Chenopodium berlandieri* (especially *C. berlandieri* ssp. *nuttalliae*, a crop of highland Mexico) and their prehistoric counterparts. Especially close morphological resemblances were noted between archaeological specimens from eastern North America and the *nuttalliae* cultivars 'chia' (a grain crop with a thin, dark seed coat) and 'huazontle' (which is harvested before fruit maturation and has small, pale-colored fruits) (Wilson 1981, 1990). Despite these similarities, in light of the absence of prehistoric records of Mexican *Chenopodium* that predate those of eastern North America a new taxon, *Chenopodium berlandieri* ssp. *jonesianum*, was created based on descriptions of well-preserved collections from Ash Cave, Ohio and Russell Cave, Alabama (Smith 1984, 1985a, 1985b; Smith and Funk 1985). This discovery was supplemented by early (ca. 1500 B.C.) accelerator dates on *Chenopodium* seeds from the Newt Kash and Cloudsplitter rockshelters in eastern Kentucky (Smith and Cowan 1987). This finding established that the widespread and economically important cultivation of this crop during the Early and Middle Woodland periods grew out of an initial development of domesticated forms during the Late Archaic.

A synthesis of information concerning the morphology and distribution (both temporal and spatial) of cultigen *Chenopodium* (Fritz and Smith 1988) concluded

that, despite the present-day existence of conspecific cultivars in Mesoamerica, the domestication of this species occurred locally and independently in the Eastern Woodlands. However, some scholars (e.g., Wilson 1981) consider it more likely that the earliest domesticated chenopod in the Eastern Woodlands was a Mesoamerican import. It is hoped that ongoing reconstruction of phylogenetic relationships among North and South American species of *Chenopodium* based on genotypic variation in living populations (Wilson 1990) will help resolve this question.

DATA AND METHODS

The data base.—Analysis of several collections of well-preserved *Chenopodium* fruits was conducted in order to detect temporal trends in seed morphology. All specimens of the cultigen type that were examined had thin, dark seed coats; the pale variety was not represented. Most of these materials represent the intensive Late Archaic and Early Woodland period occupations of several rockshelters and caves in the interior river drainages of the eastern United States (Fig. 1; Table 1). Due to exceptionally favorable conditions for the preservation of organic materials, these protected sites have been a key source of prehistoric plant remains. Study of modern samples of *Chenopodium berlandieri* was also undertaken to provide baseline data on seed morphology.

In a study of this kind, chronological placement of archaeological specimens is crucial to interpreting patterns of change and continuity correctly. For this reason, the most significant results pertain to well-dated collections. The uncalibrated radiocarbon dates reported in Table 1 are those considered contemporaneous with the collections of *Chenopodium* studied. Both samples from the Newt Kash shelter are assumed to be associated with the ca. 1500 B.C. date directly on chenopod from UMMA catalog number 16420. However, a later (ca. 700 B.C.) occupation is represented on the site as well (Crane 1956). Unfortunately, the specific context of these materials within the site is not known.

Several collections of *Chenopodium* were analyzed by the author according to the methods outlined below. In addition, data obtained from analyses by other researchers were incorporated into the present study chiefly for comparative purposes (Table 1). These sources provided important supplementary information on changing patterns of variation in *Chenopodium*. They may be consulted for more complete archaeological and methodological information.

Analytic methods.—The choice of morphological characters to be studied was made on the basis of both their relevance to the domestication process and the nature of the archaeological evidence. The thickness of the seed's outer epiderm (or testa) has the greatest utility as a diagnostic character for domesticated forms of *Chenopodium*. The testas of domesticated *Chenopodium* are significantly reduced, eliminating the extended dormancy ensured by presence of a thick, impermeable seed coat. Such a change is thought to occur because rapid germination is favored in the garden environment, in which sowing promotes crowding and increased competition between seedlings, and relatively early-maturing individuals are more likely to be chosen at harvest to contribute seed for subsequent plantings. In

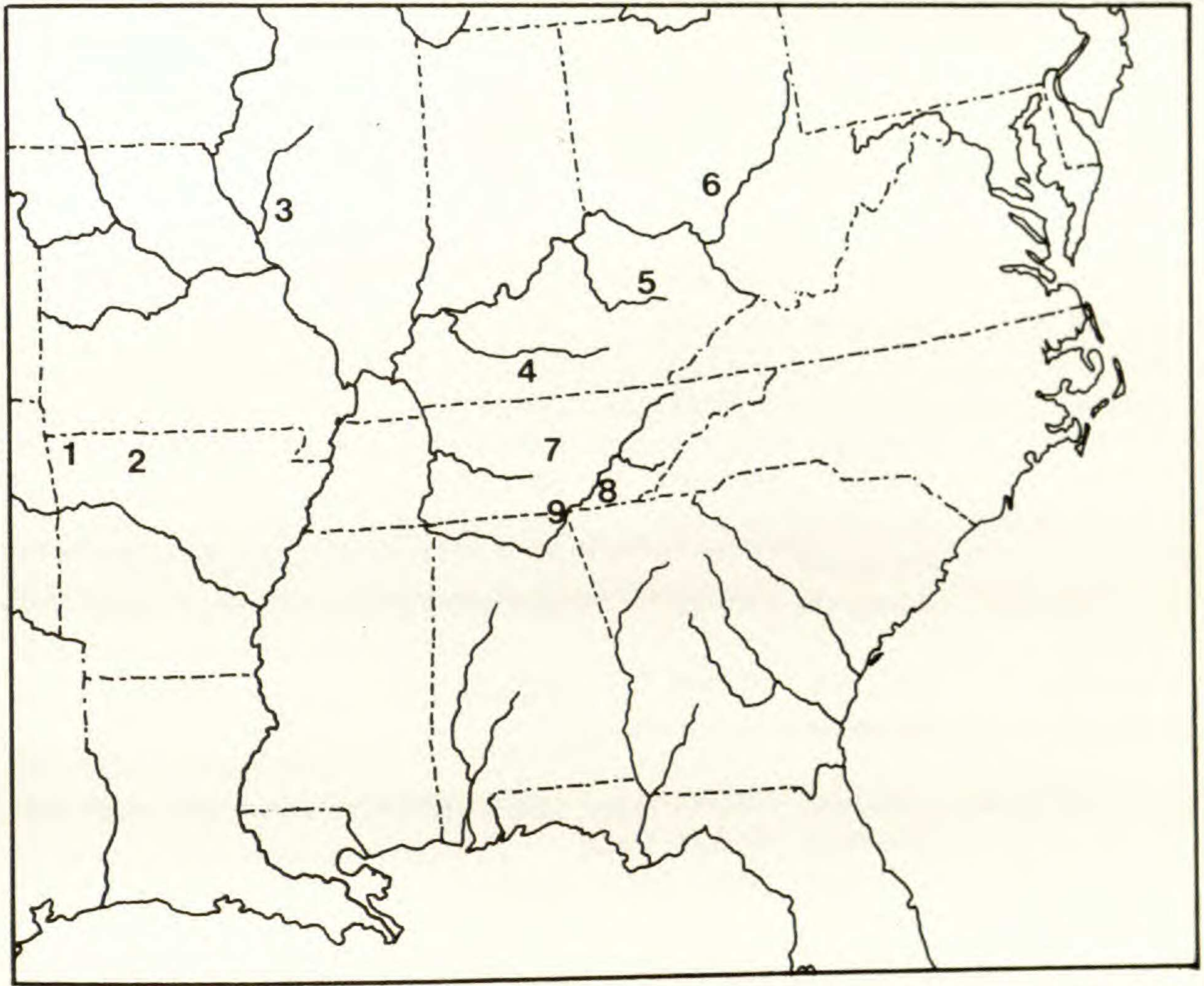


FIG. 1.—Locations of archaeological sites mentioned in text and tables. Key: 1, Whitney Bluff, White Bluff, and Edens Bluff; 2, Marble Bluff; 3, Smiling Dan; 4, Salts Cave; 5, Newt Kash, Cloudsplitter, Cold Oak, and Thor's Hammer; 6, Ash Cave; 7, Big Bone Cave; 8, Westmoreland-Barber; 9, Russell Cave.

contrast, extended dormancy or multiple germination strategies are advantageous in the wild because they increase the chances that at least some seeds will germinate when environmental conditions are favorable (de Wet and Harlan 1975:104; Harlan et al. 1973:318). Loss of the thick seed coat also removes constraints on the developing embryo, producing truncate fruit margins which contrast with the biconvex or rounded margins typical in wild populations (Smith 1985a:59; Wilson 1981:237).

A more frequently reported morphometric measurement of both archaeological and modern *Chenopodium* is seed diameter. Although this character alone cannot be used to differentiate wild from domesticated forms, seed diameter varies in a somewhat predictable fashion between members of sympatric crop/weed pairs (Gremillion 1993a; Smith 1985b). In addition, seed diameter is the character most often recorded for archaeological specimens and thus provides a large and varied data set that is useful for assessing general morphological variability.

Testa thickness of most specimens was measured with the aid of a scanning electron microscope (Cambridge S-100) located in the Scanning Electron Microscope Laboratory, National Museum of Natural History, Smithsonian Institution.

TABLE 1.—Sample information.

Source	Context	Sample ¹	Age ²	References
I. Samples analyzed by the author.				
Big Bone Cave, TN	paleofeces	Specimens 1, 2, 3, and 8	600 ± 80 B.C. ³	Faulkner 1991; Crothers 1987
Salts Cave, KY (Upper Salts)	paleofeces	SCU-140 SCU-106 SCU-41	290 ± 200 B.C.— 620 ± 140 B.C. ⁴	Watson 1974; Yarnell 1969
Salts Cave (Vestibule)	Unit KII Level 5	Flotation sample 1	250 ± 60 B.C.— 620 ± 70 B.C. ⁵	Gardner 1987
Cold Oak Shelter, KY	grass-lined storage pit	INV 124	640 ± 90 B.C. ⁶	O'Steen et al. 1991; Gremillion 1993c
Thor's Hammer Shelter, KY	storage pit	INV 23	A.D. 880 ± 70 ⁵	Gremillion 1993b
Cloudsplitter Shelter, KY	rock-lined storage cist	FS 2316	490 ± 80 B.C.	Cowan 1985a; Cowan et al. 1981; Smith and Cowan 1987
Newt Kash Shelter, KY	unknown; paleofeces	UMMA 16446, UMMA 16420	1450 ± 150 B.C. ⁶	Smith and Cowan 1987
Michoacán, Mexico (Opopeo)	cultivated "chia roja"	HDW 5113A	modern	
Mexico State (Santa Cruz)	cultivated pale-seeded	HDW 5330	modern	
II. Published data.				
Russell Cave, AL	grass-lined storage pit	F.S. 23	390 ± 120 B.C. ⁶	Smith 1985a, 1985b, unpublished notes; Fritz and Smith 1988
Ash Cave, OH	storage pit		A.D. 230 ± 100 ⁶	Smith 1985a, unpublished notes
Newt Kash Shelter, KY	various	UMMA 16440, 16441, 16444 16446, 16447	1500 B.C.— 700 B.C. ^{5,7,9}	Asch and Asch 1977; Crane 1956; Smith and Cowan 1987
Smiling Dan, IL	various		700 B.C.— A.D. 230 ^{5,7}	Asch and Asch 1985a; Sant and Stafford 1985
Marble Bluff, AR	buried in crevice	UAM 34-23-327	893 ± 44 B.C. ⁵	Fritz 1986
Marble Bluff, AR	in woven bag	UAM 34-23-341	976 ± 40 B.C. ⁸	Fritz 1986; Fritz and Smith 1988
White Bluff, AR	gourd in storage pit	UAM 32-56-17a	10 ± 105 B.C. ⁶	Fritz 1986
Edens Bluff, AR	in fiber bag	UAM 32-3-391	A.D. 20 ± 100 ⁶	Fritz 1986

Source	Context	Sample ¹	Age ²	References
Whitney Bluff, AR	in cached gourd	UAM 32-57-3a	1165 A.D. \pm 75 ⁹	Fritz 1986
	in cached grass bag	UAM 32-57-5c		Fritz 1986
Michoacán, Mexico	cultivated	HDW 5113, 5115, 5116	modern	Smith 1985b

¹Abbreviations: Sample numbers preceded by HDW were collected by Hugh Wilson; SCU = Upper Salts Cave; UMMA = University of Michigan Museum of Anthropology; UAM = University of Arkansas Museum; FS = Field Sample; INV = Inventory number.

²All radiocarbon dates are uncalibrated.

³Accelerator date obtained from one of these paleofecal specimens.

⁴Beta decay date on other paleofeces from Upper Salts Cave.

⁵Beta decay date on associated material.

⁶Accelerator date on associated *Chenopodium*.

⁷Estimate based on a series of radiocarbon dates.

⁸Beta decay date on associated *Chenopodium*.

⁹Accelerator date on associated material.

Materials from Thor's Hammer and Cold Oak were studied at a similar SEM facility in the Department of Pathology, University of North Carolina, Chapel Hill. Specimens were affixed to stubs using either double-stick tape or a solution of white water-based glue (Elvace) and water. They were then sputter-coated with a gold/palladium mixture. Most seeds were measured at a standard magnification (450 X) and working distance (36 mm) using 10 Kv illumination. Because seed coat thickness varies somewhat between regions on an individual fruit, whenever possible measurements were taken on a cross-section of the testa farthest from the "beak" (the protrusion formed by the embryonic root, or radicle) (Fig. 2a). Modern fruits were sectioned using a single-edged razor blade. Archaeological fruits, which were more fragile, were measured along an existing break.

Margin configuration was assessed by placing each seed on its narrow edge with the beak upward and observing it under low (10 x) magnification. Each seed was then placed in a category according to the form of the margin at the lowermost part of the field of view (Fig. 2b). Criteria for classification were based on illustrations in Smith (1985b, Fig. 1). It was noted that seeds might display a somewhat different margin configuration after sectioning. Consequently, all assessments of this character were made prior to sectioning in the manner described above.

Maximum seed diameter was determined to the nearest 0.1 mm using a calibrated glass slide under low magnification. Because shrinkage due to carbonization appears to reduce seed diameter by only about 5% (Smith 1985b) no corrections were made to measurements of carbonized seeds, which were restricted to the sample from Salts Cave Vestibule.

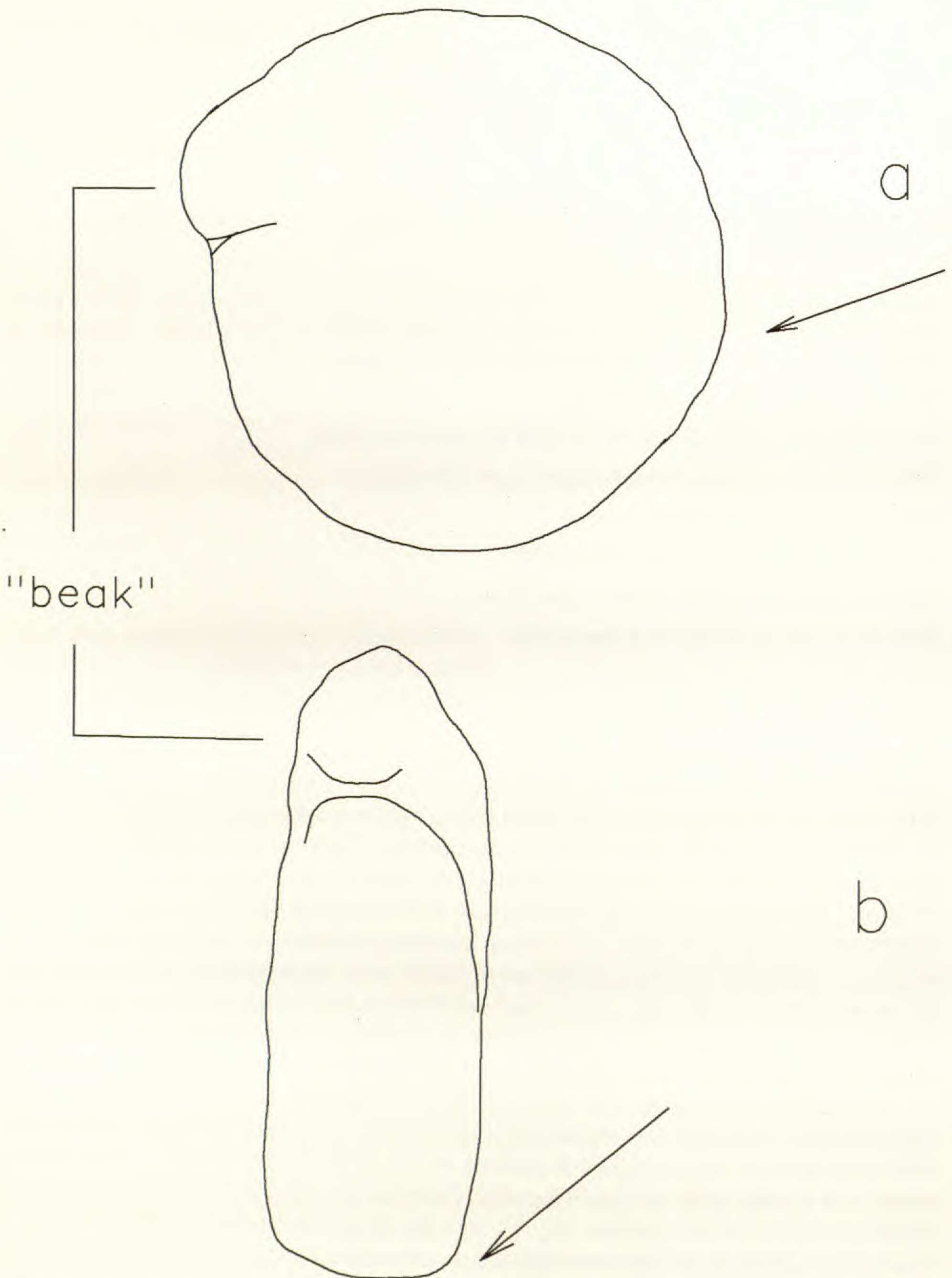


FIG. 2.—Regions of *Chenopodium* fruits selected for assessment of key characters. Arrows denote preferred locations for (a) measurement of testa thickness (dorsal view) and (b) assessment of margin configuration (lateral view with dorsal surface to the right).

Subsampling and seed categories.—In the case of archaeological *Chenopodium* seeds, all specimens from a given provenience intact enough to permit assessment of the characters described above were combined to form an analytic sample. For modern populations, mature specimens were selected randomly for analysis. Further subdivision was applied to those archaeological samples that were clearly dimorphic. The “weed morph” exhibits a suite of characteristics associated with free-living (e.g., wild and/or weedy) *Chenopodium* but not with contemporary domesticated populations. These characteristics include a thick and prominently patterned testa, lack of a prominent beak, black coloration (in uncarbonized specimens), and biconvex or rounded fruit margins. Only specimens exhibiting all of these traits were eliminated from the cultigen category. The appropriateness of this analytic distinction is supported by the statistically significant differences in diameter and testa thickness between the two morphological types (Gremillion 1993a).

TEMPORAL TRENDS IN PLANT HUSBANDRY AND CROP EVOLUTION

The fact that domestication often produces morphological change in plants has long been recognized (Darwin 1859:21). Although they vary in structural detail from species to species, the morphological traits that distinguish domesticates from their wild relatives all enhance survival and reproduction in human-managed environments. Thus, they share certain structural features related to life-cycle characteristics advantageous in these environments. These features include reduction of dormancy, enhancement of seedling vigor, and loss of natural dispersal mechanisms (Donald and Hamblin 1983). Another trend frequently recognized as an outcome of domestication is reduction of genetic variability within crop populations (Bennett 1970). This trend may reflect the relative predictability and homogeneity of the human-managed ecosystem as well as intentional selection of consistently favored traits in seedstock.

The rate and character of evolutionary change in crop populations is the product of the complex interactions between heritable traits and their phenotypic expression in particular environments. Genetic change does not necessarily result in corresponding alteration of phenotypic characteristics, and morphological variation need not represent an underlying genetic cause. Despite this imperfect relationship between the operation of selection upon seed characters and their phenotypic expression, good theoretical and empirical justification exists for linking certain aspects of morphology with selection under domestication. Thus, the archaeological record can be enlisted as one source of evidence for crop evolution.

Change in characters linked to domestication.—Reduction of germination dormancy and enhancement of stored food reserves in seeds are thought to be linked to evolution in human-managed habitats, in which early-germinating, rapidly-growing seedlings have a significant survival advantage (de Wet and Harlan 1975:104; Harlan et al. 1973:318). Thus in *Chenopodium*, the appearance of these characteristics in high frequencies implies some degree of human management. In addition, intensification of selection for these traits over time should be reflected in a gradual increase in their frequency and/or in an incremental decrease in seed coat thickness in archaeological samples.

TABLE 2.—Testa thickness statistics, domesticated *Chenopodium*.

Period	Site/Sample	Testa Thickness (Microns)			
		Mean	S.D. ¹	C.V. ²	n
Late Archaic (1500–1000 B.C.)	Newt Kash (16420)	15.8	2.0	12.7	10
	Newt Kash (16446)	20.7	11.7	56.4	10
Early Woodland (1000–300 B.C.)	Salts Vestibule	10.5	5.5	52.8	11
	Upper Salts	13.3	4.9	37.1	38
	SCU-140	13.8	4.8	34.6	8
	SCU-106	13.9	5.7	41.2	20
	SCU-41	11.7	3.0	25.6	10
	Cold Oak	13.0	2.6	30.9	14
	Cloudsplitter	13.0	2.6	20.3	14
	Russell Cave	11.3	2.8	23.8	20
	Big Bone Cave ³	21.2	4.7	22.3	35
Middle Woodland (200 B.C.–A.D. 500)	Ash Cave	14.9	3.0	20.3	20
Late Woodland (A.D. 500–1000)	Thor's Hammer	13.9	4.9	35.5	21
Modern cultivars	HDW 5113, 5115	16.3	3.8	23.1	20
	HDW 5113A	18.6	3.5	18.6	10

¹s.d. = Standard deviation

²c.v. = coefficient of variation

³Specimens 1, 2, and 3.

Early prehistoric domesticated chenopod from the Eastern Woodlands varies in the extent to which it reflects selection for reduced dormancy during incipient stages of domestication (Table 2). One sample from Newt Kash shelter (UMMA 16446) displays relatively high mean testa thickness values. Similarly, *Chenopodium* from Marble Bluff shelter in northwestern Arkansas dating to ca. 1000 B.C. was described as having somewhat thicker seed coats than later collections (Fritz 1986:83). Both samples are among the most ancient that have been studied. On the other hand, some of the material from Newt Kash and Cloudsplitter compares favorably in overall morphology with modern Mexican cultivars. Thus, although some early material resembles wild forms (whose testa thickness typically averages above 40 microns; Smith 1985b), other collections (including the earliest known thin-testa fruits) are virtually indistinguishable in this respect from modern cultivars.

The absence of a directional trend is demonstrated by the correlation between testa thickness and estimated sample age for data in Table 2, which is near 0 ($r = -0.05$, $p = 0.88$, $N = 12$) (Fig. 3a). Thus, there is no evidence that seed coat thickness was reduced in a gradual, linear fashion in the past. Throughout the Woodland period (ca. 1000–300 B.C.), mean testa thickness values remain primarily in the 10–20 micron range. In fact, no archaeologically visible changes in this character are

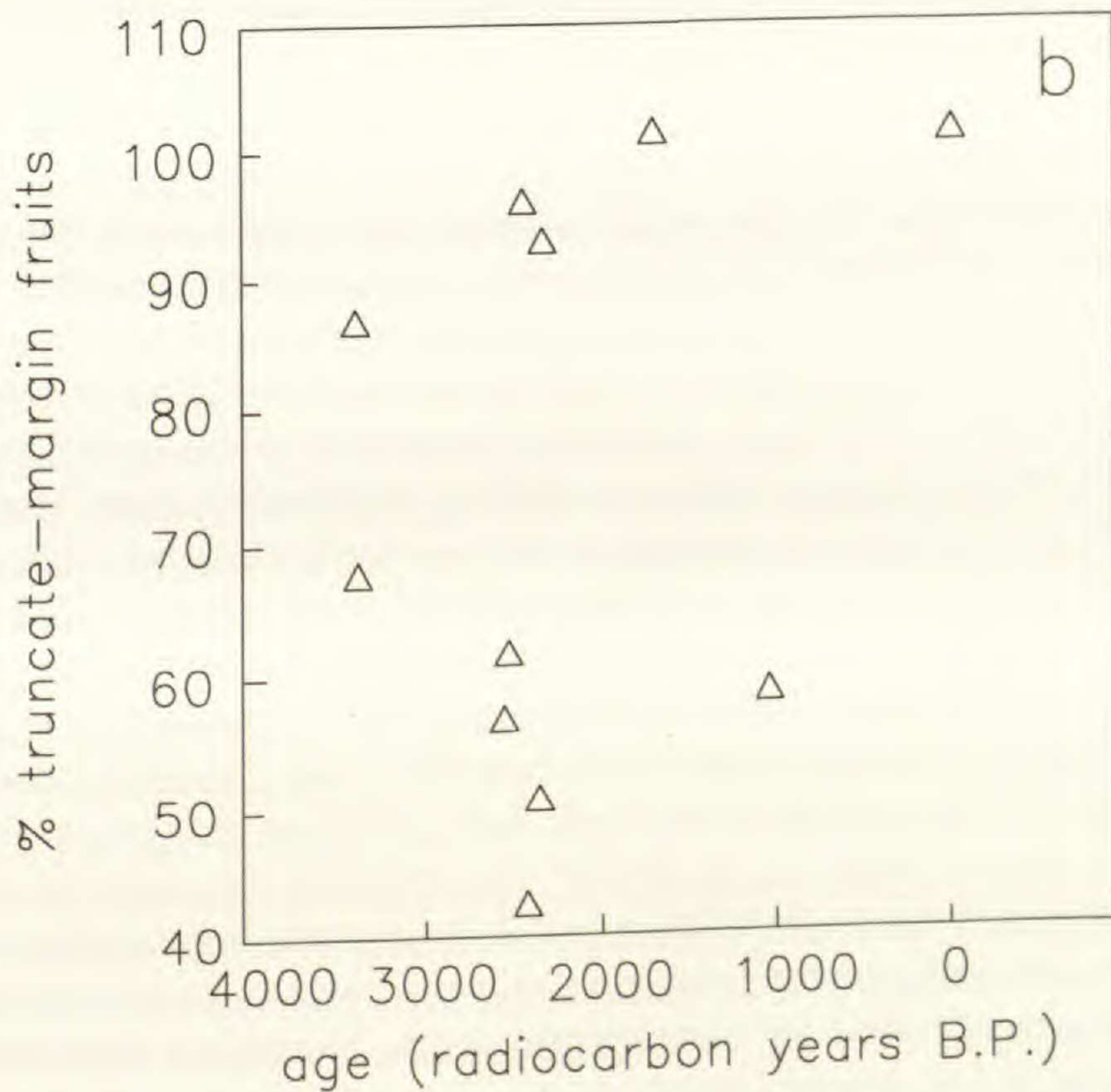
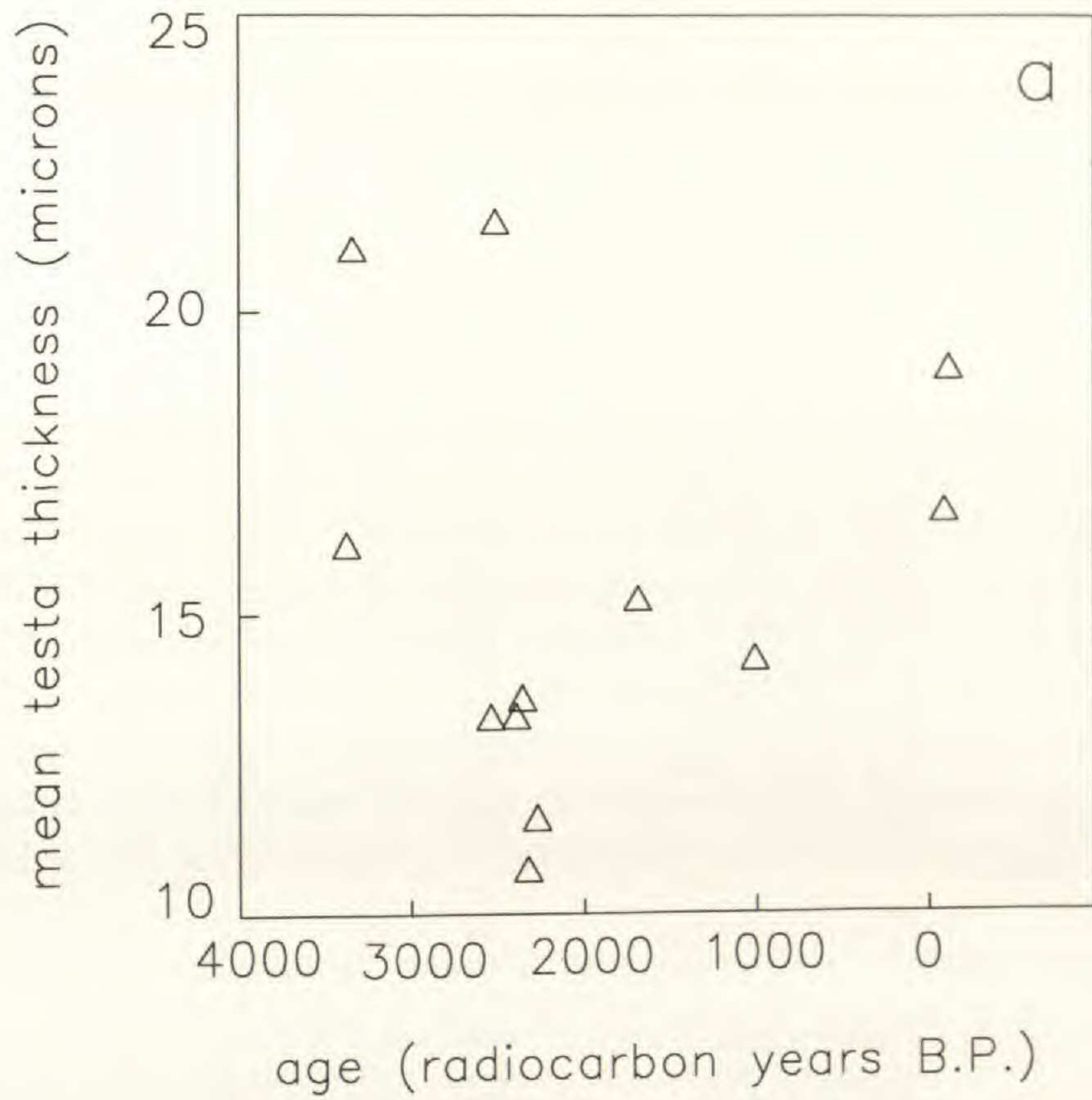


FIG. 3.—Plots of sample age against (a) mean testa thickness and (b) percentage truncate-margin fruits for collections of cultigen chenopod. (a) $n = 12$, $r = -0.05$, $p = 0.88$; data appear in Tables 1 and 2; (b) $n = 12$, $r = -0.42$, $p = 0.18$; data appear in Tables 1 and 3.

TABLE 3.—Margin configuration types, domesticated *Chenopodium*.

Period	Site/Sample	Margin Configuration (percentage of specimens) ¹					
		T	T/R	R	E/B	B/A	N
Late Archaic (1500–1000 B.C.)	Newt Kash (16420)	67	13	20	—	—	15
	Newt Kash (16446)	86	10	3	—	—	29
Early Woodland (1000–300 B.C.)	Salts Vestibule	50	17	33	—	—	6
	Upper Salts	42	11	38	9	—	90
	Cold Oak	56	19	18	7	—	134
	Cloudsplitter	95	3	2	—	—	62
	Russell Cave	91	—	2	7	<1	387
	Big Bone Cave	61	15	24	—	—	33
Middle Woodland (200 B.C.–A.D. 500)	Ash Cave	100	—	—	—	—	24,856
Late Woodland (A.D. 500–1000)	Thor's Hammer	58	13	14	15	—	122
Modern cultivars	HDW 5330	100	—	—	—	—	50
	HDW 5113A	100	—	—	—	—	50

¹T = truncate; T/R = truncate/rounded; R = rounded; E/B = equatorial banded; B/A = biconvex acute.

apparent until the development of pale-seeded varieties as early as ca. A.D. 300 (Fritz and Smith 1988).

Like testa thickness, margin configuration also appears to be sensitive to human-mediated environmental change. This character (quantified as percentage of truncate-margin fruits) exhibits a stronger but still not statistically significant relationship to time period ($r = -0.42$, $p = 0.18$, $N = 12$; see Table 3 for data) (Fig. 3b). Unlike testa thickness, however, frequency of margin configuration types in most archaeological samples differs markedly from that found in modern cultivars. Collections dating to before about 500 B.C. exhibit a wide range of variation in percentage of fruits with truncate margins. Only after that time do some samples (e.g., Cloudsplitter) replicate the 100% truncate pattern typical of modern Mexican cultivars. However, this contrast may simply reflect the disparity between archaeological and modern sample derivation; only the modern material is known to have been derived from single plants or populations.

The absence of a clear directional trend in morphological change for *Chenopodium* contrasts with patterns observed in sunflower and sumpweed, in which seed size is the key criterion for domesticate status. Summary data for those taxa indicate a steady, if not entirely linear, increase in achene size beginning as early as ca. 2000 B.C. (Smith 1987, Fig. 1-2). This gradual process appears to intensify around A.D. 500 for both species, with seed size curves rising sharply thereafter. The acceleration of seed size increase in sunflower and sumpweed is roughly contemporaneous with the establishment of farming economies in the Eastern Woodlands and the widespread appearance of cultigen remains in storage con-

texts. Thus, both trends are probably related to the intensification of plant management techniques such as careful selection of seedstock.

What factors might account for this difference in the evolutionary pathway taken by chenopod and two species with which it probably coexisted in prehistoric gardens? One potentially important variable is the genetic basis of seed morphology in these taxa. In *Chenopodium*, seed coat thickness is highly plastic. Although this character is under some degree of genetic control, in some *Chenopodium* species its expression is environmentally triggered (Harper et al. 1970; Williams and Harper 1965). Thin-testa fruits are present in minor frequencies in wild populations of *C. berlandieri/bushianum* and in certain environmental contexts they are numerically dominant (Asch and Asch 1977). This plasticity may have provided a basis for the very rapid establishment of the thin-testa trait at high frequencies in early protodomesticated populations (Asch and Asch 1985b). The subsequent evolutionary success of domesticated populations would have been ensured given some degree of heritability of the thin-testa/rapid germination trait complex.

Species-specific inheritance patterns and population biology may thus explain the initial rapid establishment of morphologically distinctive populations of *Chenopodium*. Somewhat more difficult to explain is the apparent absence of a gradual trend toward increasingly thinner seed coats paralleling the seed size increase in sunflower and sumpweed. However, several contributing factors can be identified. First, there is no reason to assume that an infinite number of intermediate character states are possible for testa thickness in all *Chenopodium* populations. Instead, limitation to only a few alternative phenotypes may have rendered selection for increasingly thinner testas impossible. Second, phenotypic plasticity is a complicating factor. Because the alternate phenotypes in wild *Chenopodium* do not necessarily reflect underlying genetic differences, removal of one morph from a population would not prevent its reappearance in subsequent generations (Harper et al. 1970:341). In practical terms, selective planting of thin-testa fruits will not immediately result in elimination of wild-type seeds. Thus although some genetic control of seed morphology in *Chenopodium* can be assumed, the plasticity of key seed characters with respect to environmental variables may have acted to buffer directional selection (Harper 1977:72).

Morphological heterogeneity.—It has frequently been noted that genetic diversity is lower in domesticated plants than in their wild relatives, a difference that is accentuated by modern economic development geared toward maximizing yields (Baker 1972:34; Bennett 1970:121, 124; Brush et al. 1988; Harlan 1975:163–167). Diversity increases under domestication primarily by way of the development of morphologically distinct cultivars or in the form of persistence of highly divergent varieties that would be selected against in the wild (Harlan 1975:109–110). Thus although domesticated species may be taxonomically diverse, individual cultivar populations tend to be rather uniform. Selective breeding, separation of cultigens from related wild populations, and (in modern times) introduction of highly uniform seedstock are responsible for these patterns. Thus, if morphological variability is found to remain high throughout the sequence represented by archaeological material, practices such as isolation and selective breeding were

TABLE 4.—Fruit diameter statistics, prehistoric domesticated *Chenopodium*.

Sample	Maximum Fruit Diameter (mm)			N
	Mean	S.D.	C.V.	
Newt Kash (16420)	1.96	0.17	8.67	18
Big Bone Cave	1.79	0.13	7.00	52
Salts Cave Upper	1.75	0.17	9.62	104
Cold Oak	1.81	0.15	8.28	135
Thor's Hammer	1.79	0.23	12.81	127
Cloudsplitter	1.80	0.13	7.51	62
Russell Cave	1.32	0.13	9.84	525
Ash Cave	1.87	0.15	8.02	1,000
Newt Kash (misc.)	1.88	0.21	11.17	85
Smiling Dan	1.57	0.15	9.56	24
Marble Bluff (341)	1.48	0.17	11.49	26
Marble Bluff (327)	1.60	0.17	10.63	200
White Bluff	1.58	0.10	6.33	100
Edens Bluff	1.66	0.11	6.63	125
Whitney Bluff (3a)	1.90	0.13	6.84	73
Whitney Bluff (5c)	1.82	0.16	8.79	55
Newt Kash (16446)	1.74	0.17	9.59	31
Salt Cave Vestibule	1.46	0.14	9.78	9

probably limited in frequency or degree. Reduced variety within samples over time will instead indicate some intensification of these practices.

In order to evaluate the hypothesis that domesticated chenopod became less morphologically variable over time, coefficients of variation were computed for testa thickness (Table 2) and diameter (Table 4). The coefficient of variation (standard deviation/mean \times 100) is a useful measure of variability within a sample because it expresses standard deviation as a percentage of the mean. If later populations were less morphologically homogeneous than earlier ones, they should have significantly lower coefficients of variation for traits such as testa thickness. In addition, fruit size, although not a valuable yardstick for domestication, might be expected to show a similar reduction in variability.

For purposes of this analysis, the age of each sample was based upon available radiocarbon determinations (Table 1). When necessary, series of dates were converted to estimates by averaging the two extreme values. Modern specimens were eliminated from this analysis because of the likelihood that differences in variability between modern and prehistoric samples are partly attributable to factors other than chronological placement and the evolutionary processes thus implied. For example, modern samples were generally derived from single plants or populations, whereas the origin of archaeological material remains unknown and, thus, may represent a much larger and more varied gene pool.

Only a weak correlation between testa thickness coefficient of variation and sample age was noted for domesticated *Chenopodium* ($r = 0.28$, $p = 0.38$, $n = 12$) (Fig. 4a). Initial results similarly revealed no significant correlation between seed

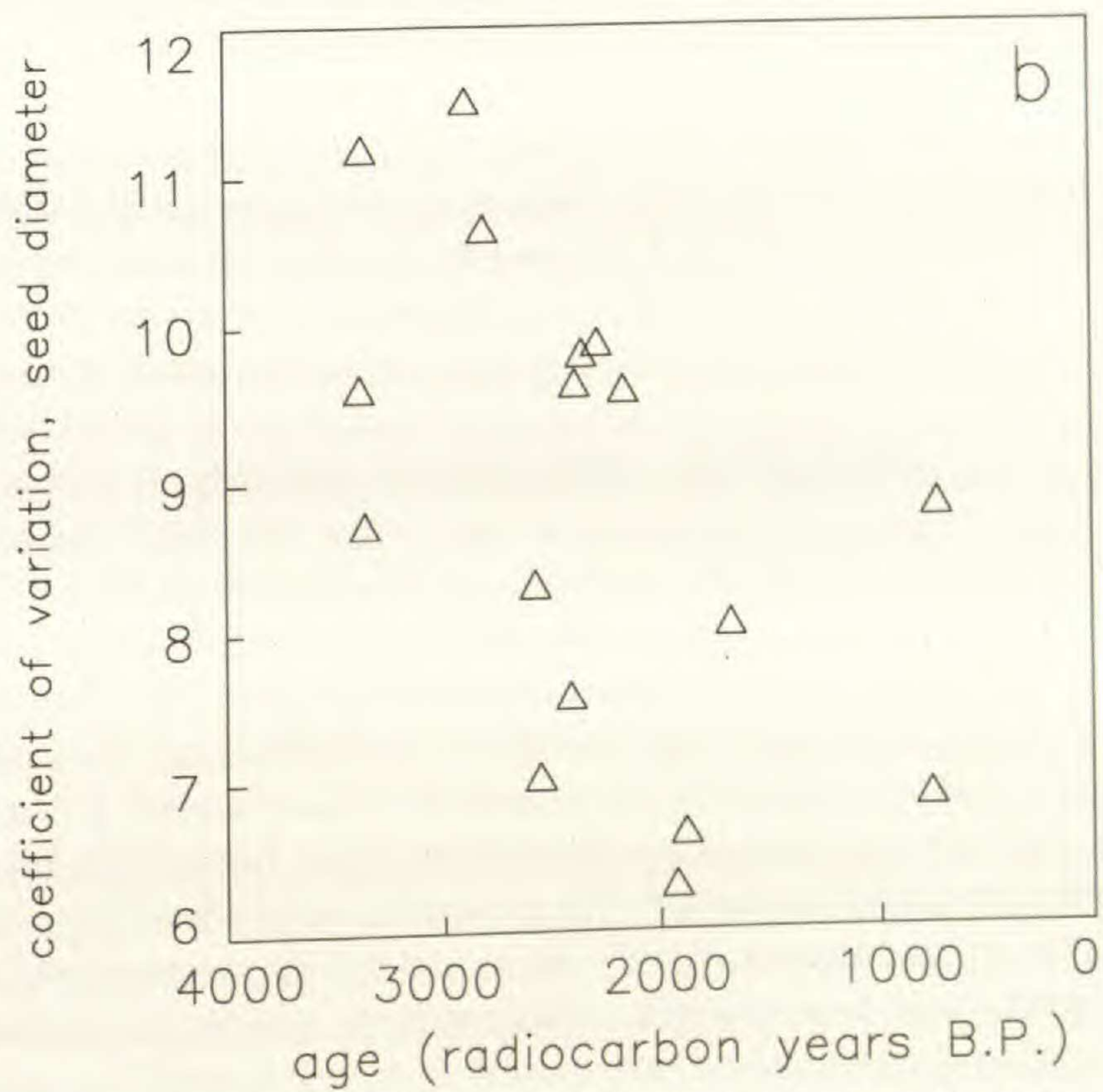
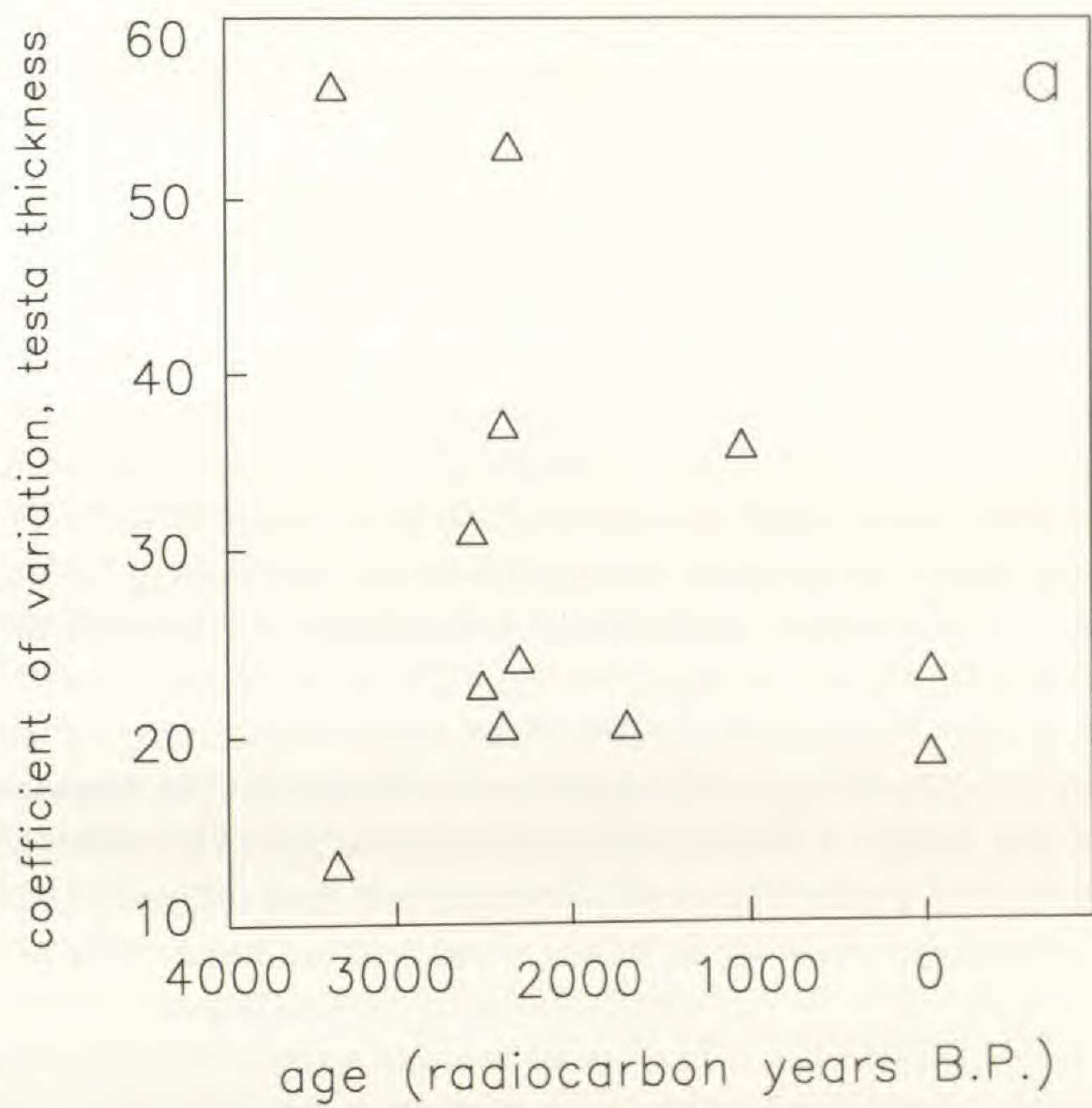


FIG. 4.—Plots of sample age against coefficient of variation for (a) testa thickness and (b) seed diameter for collections of cultigen chenopod. (a) $n = 12$, $r = 0.28$, $p = 0.38$; data appear in Tables 1 and 2. (b) $n = 17$, $r = 0.53$, $p = 0.03$; data appear in Tables 1 and 4; Thor's Hammer outlier omitted from an original sample of 18 collections.

diameter coefficient of variation and sample age ($r = 0.22$, $p = 0.37$, $n = 18$). However, analysis of residuals revealed the presence of an outlier. Removal of this case (Thor's Hammer) greatly strengthened the association between the two variables ($r = 0.53$, $p = 0.03$, $n = 17$) (Fig. 4b). Thus, comparison of coefficients of variation for two seed characters provide some support for the contention that domesticated populations of *Chenopodium* became less morphologically variable over time.

The persistence of a high degree of morphological variety in domesticated *Chenopodium* despite some tendency toward greater uniformity in seed size may be related to the presence of traits characteristic of free-living forms in cultigen gene pools. The "weed morph" sometimes identified in archaeological collections coexisted throughout much of prehistory with its cultigen counterpart (Gremillion 1993a). It has been argued that these seed categories represent distinct populations, each maintaining a different set of adaptations to human disturbance (Gremillion 1993a; Smith 1985b). Although reproductively isolated to a large extent, crop and weed populations of *Chenopodium* may have hybridized. These inferences are supported by the thickness of the seed coat in the archaeological weed morph (which tends to be intermediate between that of wild and domesticated forms) and by patterns of variation in seed size that resemble those obtained from contemporary crop/weed pairs of *Chenopodium berlandieri* (Gremillion 1993a; Smith 1985b). Additionally, the relatively high mean testa thickness of crop-type *Chenopodium* from sites such as Big Bone Cave may reflect gene flow between divergent populations. Such interaction would have interfered with any tendency for characters such as testa thickness, fruit shape, and fruit size to become canalized along certain lines. Maintenance of homogeneous cultivars would have been a particular challenge for *Chenopodium*, which is not only wind-pollinated but is represented by a series of wild and frequently interfertile taxa over most of the Eastern Woodlands. Similar difficulties for sumpweed (Cowan 1985b) may have been ameliorated by the more restricted geographical range of wild conspecifics.

DISCUSSION AND CONCLUSIONS

Several conclusions about the evolution of *Chenopodium* as a domesticate in eastern North America emerge from this examination of diachronic variation in morphology. The first of these center around the process of domestication and how it varies with the ecological and genetic characteristics of the plants involved. The evolutionary pathway taken by *Chenopodium* contrasts with patterns observed for two other indigenous seed crops known to have been domesticated before 1500 B.C., sunflower and sumpweed. For example, no gradual long term changes in the expression of traits most closely linked to the domestication process (e.g., seed coat thickness and fruit margin configuration) can be documented. In contrast, sumpweed and sunflower both exhibit a trend toward increasing achene size over some two millennia (Fritz 1986; Smith 1989; Yarnell 1972, 1978). In *Chenopodium*, initial human-mediated environmental changes caused thin-testa fruits to have a selective advantage in gardens. Perhaps due to the presence of the thin-testa phenotype in wild populations, that trait became quickly established at high frequencies. Thereafter, mean testa thickness remains fairly constant over many

centuries. Thus, a relatively sudden shift in the traits most closely linked to selection in human-modified habitats occurred rather than gradual, incremental change. Equally abrupt as measured by archaeological data is the appearance of the pale cultivar, which seems to be the next important landmark in *Chenopodium* evolution.

Heterogeneity (as measured by variation in fruit size and testa thickness within archaeological samples) similarly shows only a weak tendency to decrease as agricultural systems evolved. The seed characters most closely associated with domestication, testa thickness and margin configuration, change little over time. On the other hand, variability in seed size does seem to have been significantly reduced, perhaps reflecting the development of simultaneous ripening or some related outcome of the domestication process. Despite this evidence for increasing control over *Chenopodium* populations, the generally high degree of morphological variability in prehistoric *Chenopodium* may indicate that techniques of plant management were still in an incipient stage of development. It may also reflect hybridization between crop and weed populations in small gardens whose diverse plant communities were managed by humans in a relatively casual fashion. By analogy with small-scale agricultural systems of the present day, plant husbandry led to the evolution of landraces and cultivars (such as the pale forms) over a broad region. However, the occurrence of weed forms suggests that Woodland period peoples of the eastern United States also faced many of the same challenges that are involved in maintaining the integrity of modern varieties. These include the propagation of crop strains with desirable characteristics, the management of noncrop species sharing the agricultural habitat, and the effective storage of seed.

Environmental uncertainty may also have limited the degree of homogeneity reached by developing crops, even in the context of human protection and management. Increasing human control over the plant habitat reduces the selective advantage of flexibility by diminishing environmental uncertainty (Rindos 1984: 185). Flexibility of response to environment, which is itself under genetic control (Bradshaw 1965:119), is therefore expected to decrease under domestication; in contrast, phenotypic plasticity characterizes the typical weed strategy (Baker 1974:8; Bradshaw 1965:127–128). The relative predictability offered by human management is also prerequisite to the loss of genetic variability that occurs under domestication, which limits the plant population's ability to cope successfully with a wide range of environments (Bennett 1970:124). The fact that cultigen forms of *Chenopodium* remained morphologically variable thus suggests that agricultural habitats were not managed rigorously enough to eliminate the advantages of flexibility of response at both the individual and population levels.

Despite the general absence of gradual change in *Chenopodium* morphology, the timing of the appearance of distinctive forms and chronological patterning in the representation of various margin configuration types provides some basis for a reconstruction of the evolution of this crop. Thin-testa *Chenopodium* at ca. 1000 B.C. was still somewhat variable in margin configuration and seed coat thickness, although clearly outside the range of modern wild populations. However, the earliest known collections also include forms quite similar to modern Mexican cultivars. The morphological evidence is thus consistent with both the convergent evolution and single origin hypotheses for the domestication of *C. berlandieri*;

however, the latter interpretation is weakened by the failure to identify any second millennium B.C. source for this hypothesized northward dispersal (Fritz and Smith 1988:13). Two additional types of *Chenopodium* become visible in the archaeological record between 500 B.C. and A.D. 300: the weed and the pale cultigen. Distinctly dimorphic collections composed of both weed and cultigen seed types do not predate the establishment of domesticated *Chenopodium* as an abundant component of seed assemblages. Patterns of archaeological occurrence of the weed form may therefore indicate increasing environmental disturbance and the simultaneous creation of garden habitats. Continuing hybridization with weed forms (as at Big Bone Cave), as well as regional diversity in the tempo of the evolution of the crop, is also reflected in Early and Middle Woodland collections. Beginning around the same time (or perhaps earlier), farmers were able to maintain cultivars that were fully dependent upon human management for survival. The fact that these pale forms did not appear earlier suggests that their establishment as crops awaited the development of more effective husbandry and/or storage techniques.

Chenopodium reached its height of popularity as a crop at different times in different areas. In eastern Kentucky rockshelters, it played an important role in small-scale agriculture as early as ca. 500 B.C. (Gremillion 1993c). In west central Illinois, its seeds are most abundantly represented in the form of charred masses from Late Woodland contexts, although they are also an important component of starchy seed assemblages from earlier periods (Asch and Asch 1985b:183). A similar pattern appears in the American Bottom and southward to the Arkansas River valley, where *Chenopodium* and other native starchy seed crops peak in abundance only after about A.D. 500 (Fritz and Kidder 1993; Johannessen 1984). *Chenopodium* continued to be an important crop in many parts of the Eastern Woodlands well into the Late Prehistoric period (after A.D. 1000), although by that time it (along with other native crops) had been largely displaced by maize in the Middle Ohio Valley (Wagner 1987). In the Ozark uplands, *Chenopodium* first became an important crop during the first centuries A.D. and continued that role until at least A.D. 1200 (Fritz 1984, 1986). Groups in the lower Mississippi Valley and the mid-Atlantic coast apparently still grew *Chenopodium* at the time of European contact (Asch and Asch 1977; Harriot 1972). Interestingly, after about A.D. 500, weed forms are found more abundantly in contexts suggesting heavy utilization. For example, at the Westmoreland-Barber site in southeastern Tennessee large quantities of weedy *Chenopodium* were deposited along with maize remains in a deep refuse-filled pit dated to ca. A.D. 600 (Gremillion 1993a; Gremillion and Yarnell 1986).

Morphological analysis of prehistoric crop remains, though limited in some respects, has significant value as an empirical basis for inferences about garden ecology and plant husbandry practices. By exploring relationships between morphological change, selection, and human behavior, it is possible to construct hypotheses regarding the past relationships between human and plant populations. Although the present analysis is limited to a single species, it reflects to some extent general horticultural patterns. It is hoped that studies of other taxa represented archaeologically, along with continued analyses of genetic and morphological variation in modern populations, will continue to enhance our knowledge of prehistoric agriculture in the Eastern Woodlands of North America.

NOTE ON CURATION

All samples analyzed by the author are currently curated at the Paleoethnobotany Laboratory, Department of Anthropology, The Ohio State University, except for material from Big Bone Cave, which is held by the Tennessee Department of Conservation. Materials from the Cold Oak shelter and Thor's Hammer shelter are to be permanently curated at the University of Kentucky Museum of Anthropology.

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